Reference: *Biol. Bull.*, **145**: 548–564. (December, 1973)

NATURAL HISTORY OF THE HYDROCORAL *ALLOPORA CALIFORNICA* VERRILL (1866) [1]

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The hydrocoral *Allopora californica* Verrill (1866) is one of many spectacular, but little known organisms living subtidally off the central California coast. Until recently its habitat frustrated attempts at scientific investigations for dense kelp beds and the rocky reefs in the area made dredging difficult. Even when specimens were dredged, it was hard to envision the environment from which they had come. Of course there was no way to revisit the same coral colonies repeatedly, so long-term investigations were not possible. Not until SCUBA (Self Contained Underwater Breathing Apparatus) was developed could this rich environment be opened to direct scientific investigation. Using this research tool, this study of *Allopora californica* was undertaken, the first attempt to observe the living hydrocoral in its normal undisturbed situation underwater. The life history, settlement and mortality of new colonies, and regeneration were studied.

Materials and Methods

SCUBA procedures

All dives were made with a "buddy," thanks to the willing help of many University of California certified divers, and all diving procedures were in accordance with the U. C. Berkeley Diving Safety Manual. The dives were "no-decompression" dives conforming to the U. S. Navy Air Decompression Tables (U. S. Navy Diving Manual, 1963). The study extended from November 1968 through May 1971 except for the period from October 1969 through December 1969 when the Carmel beaches were closed as a result of serious pollution from sewer outfalls.

Research sites

The two research sites were 15–20 meters deep, one off Carmel River Beach, Carmel, California, and the other in Bluefish Cove at Point Lobos State Reserve, Carmel, California (Fig. 1). Each site was marked with a surface float to facilitate relocation. The underwater areas were mapped making it possible to swim to any part of the site, even when underwater visibility was limited to a few meters (Little, 1971).

At each site large, irregularly shaped rocky reefs rise 3 to 5 meters above a sand or rubble bottom. The tops of the reefs are about 15 meters deep, while the sandy bottoms are about 20 meters deep. *Macrocystis integrifolia* is the dominant

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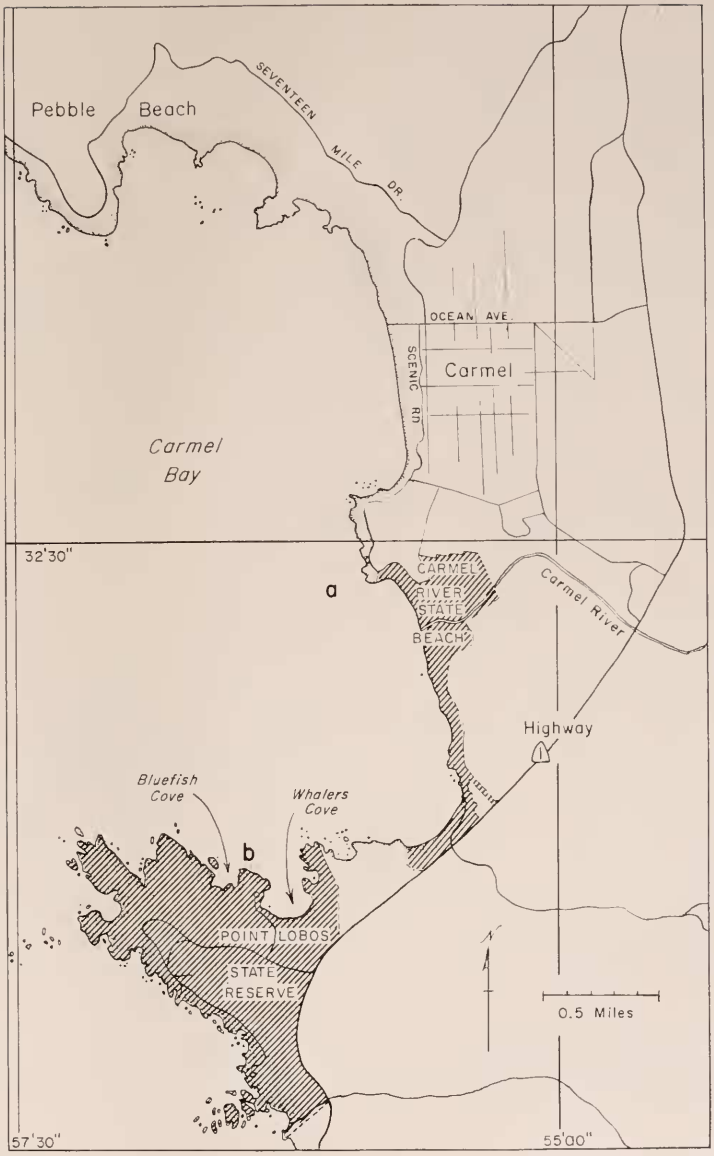

FIGURE 1. Map of Carmel Bay, Carmel, California, showing the location of the two research sites; (a) Carmel River Beach research site, (b) Bluefish Cove research site.

alga. Various small red, brown and coralline algae cover the tops of the reefs during certain seasons of the year. The research areas are rich in invertebrate life with many species present. Some of the more delicate sponges, bryozoans, tube worms, *etc.* are common here. Several open-water rock fish, *Sebastes* spp., are seen, as well as many of the bottom-dwelling territorial species.

Life history study

For the study of the reproductive cycle, specimens of coral were collected approximately monthly from both sites. A small branch was collected from each of 20 tagged colonies and from a few randomly selected colonies. As soon as possible after returning to the beach, the samples were relaxed for 1–2 hours in sea water with a few menthol crystals sprinkled on the surface, killed with 1–2% formalin, in sea water (10 minutes), then fixed in Bouin's picroformalin fixative or Susa's mercuric-chloride fixative. The coral was decalicified using daily changes of the fixative. A week to 10 days was usually required.

When the skeleton had been decalcified, a gross examination was made with the aid of a Wild dissecting microscope. The size of the piece was determined, the number of cyclosystems counted, and then, if the sample were female, the tissue was teased apart to pick out the eggs. These were counted and measured to obtain an average size. If it were a male colony, the general condition of the sperm sacs was recorded. A second piece of the same branch was then processed for paraffin sectioning using cedarwood oil as a clearing agent to help soften the yolky tissue. Sections were cut at 8 μ, stained with Heidenhain's iron hematoxylin, and occasionally counter-stained with eosin Y or fast green. From these slides the state of the development of the reproductive products was determined.

Settlement and mortality of new colonies

In order to study larval settlement and subsequent survival a recruitment-mortality study was made. A definable rock surface was chosen and a reference piton driven in. A measuring line with distances marked was used to measure the distance from the piton to each colony on the rock. A plastic protractor, fitted with a clip which slipped over the piton, was used to measure direction. For each colony two coordinates were recorded: a distance and a direction in degrees relative to the reference piton. An underwater slate was used to record the data (Little, 1971). When checking the study areas, previously existing colonies were located and the positions of new colonies were added to the slate. An underwater light was indispensible for spotting the tiny new colonies. Eight study plots, four at each research site, were studied for almost two years with counts made every 1–2 months.

The size of these irregular plots was determined by measuring the distance and direction from the reference piton to the edge of the rock at several points. This information was transferred to graph paper and, when the outline was drawn, the area could be estimated.

Regeneration

For the regeneration study, large colonies of *Allopora* were tagged and 5–10 separate branches were snapped off. Close-up photographs of the cut ends (1:1 subject:image ratio) were taken periodically to assess the extent of regeneration. All underwater photographs in the study were taken with a Nikonos 35 mm underwater camera with a Nikonos flash attachment, on Kodachrome X film (ASA 64), using Sylvania 26B or General Electric 6B flashbulbs. For a 1:1 subject:image ratio a commercially available extension tube was used with the 35 mm lens.

In addition to the photographic record made in the field, regeneration was studied histologically. At various intervals cut branches were recut. These were fixed, decalcified, and sectioned in paraffin for light microscopy as described previously. By examining these sections it was possible to trace the healing of the cut surfaces and the development of new cyclosystems as the branches regenerated

Results

General structure

Allopora californica is abundant in parts of Carmel Bay at depths of 10–30 meters. Living colonies may be pink, ranging from a very light pink to a light red, or they may be various shades of purple. The largest are 30 cm high and may be 30 cm in diameter. The growth form is variable, sometimes as regular as a hemisphere in shape, but usually displaying an irregular branching pattern. The rows of branches tend to grow perpendicular to the prevailing currents (Roth, 1969).

On the colony surface the openings, or cyclosystems, are visible. These pores each contain a single gastrozooid, or feeding polyp, plus 4–8 dactylozooids, which

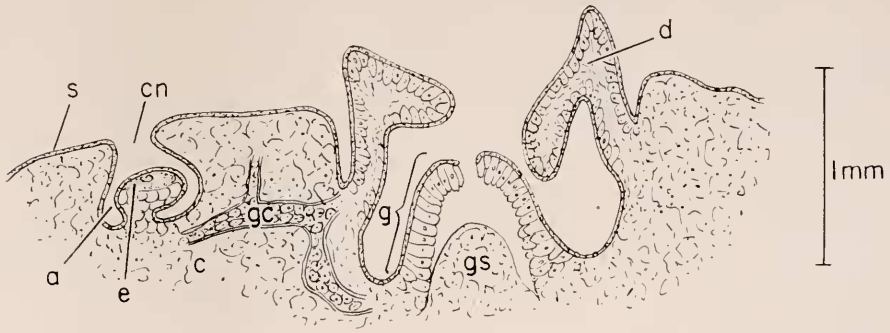

Figure 2. Diagram illustrating a typical longitudinal section through a cyclosystem of *A. californica*. Abbreviations used are: a, ampulla; c, calcareous skeleton; cn, canal opening to the surface of the colony; d, dactylozooid; e, egg; g, gastrozooid; gc, gastrodermal canals; gs, gastrostyle; s, surface of the colony.

are protective and food-capturing polyps. In a longitudinal section through the gastrozooid and dactylozooids, the cyclosystem appears as indicated in Figures 2 and 3.

The gastrozooids are 0.5–1 mm deep in the cyclosystems, each located on a calcareous spine, the gastrostyle. The gastrozooids have four tiny, seemingly useless tentacles around the mouth. The surrounding dactylozooids are also located atop calcareous structures, the dactylostyles. The mouthless dactylozooids can extend and reach 1–2 mm above the surface of the colony to capture food. Connecting the different zooids and cyclosystems within a colony there is a series of tortuous canals composed of gastrodermis with a thin epidermal covering. The mesolamella between the two layers is acellular and extremely thin. Presumably nutrients and waste products can be moved via the gastrodermal canals. The living tissues, the

zooids and canals, are found primarily in the outer 2–4 mm of the colony. Calcified material fills the spaces not occupied by the living tissue. The inner core of the colony is calcified material with only a few strands of living tissue running through it.

A second type of dactylozooid is also present. These are not part of a cyclosystem; rather, they are found singly in chambers scattered at random throughout the colony between cyclosystems. The function of these zooids is not known for certain, but they are the first to expand after the colony has been disturbed, suggesting either a sensory or a protective role.

The male and female reproductive structures or gonophores develop in epidermally-lined cavities, the ampullae. These are generally smaller and more numerous in male colonies.

Three obligate commensals have been reported on *Allopora*, a barnacle, a polychaete worm, and a snail. The barnacle, *Balanus nefrens* Zullo (1963), settles on the surface of the colony. The coral grows over the barnacle leaving only the opening at the top exposed. Most colonies have several barnacles on them, forming pyramid-shaped growths along the sides of the branches.

A second commensal is the spionid worm, *Polydora alloporis* Light (1970). The worms burrow longitudinally through the central calcareous core of the branches, secreting tubes lined with calcareous material. Paired openings to the tubes are found scattered over the surface of the coral colony. Almost every colony found was infested with worms, sometimes so many that the skeleton was weakened and more susceptible to breakage.

On rare occasions, a third commensal, the ovulid snail *Pedicularia californica* Newcomb (1868), was found on *Allopora*. The snail's shell always matched the color of the host colony. On repeated visits to the same colony, the snail was always found in exactly the same place, a slight depression on the surface of a branch exactly the right size and shape to accommodate the margin of the snail's shell. No living cyclosystems were found in this area. Either *Pedicularia* does not move or it always returns to the same position on the branch of coral.

Reproductive cycles

Each colony of *Allopora californica* is either male or female. This cannot be determined in the field; the colony must be dissected or sectioned to determine its sex.

From the histological data the development of the female gonophore, the egg, and the planula was observed. The eggs grow, are fertilized, and develop in the ampullae. These cavities originally form at the lateral margins of the colony. Epidermis and gastrodermis meet, and the cell layers thicken. The branch continues to increase in diameter while the area around the thickening remains fixed, giving the impression that the young ampulla is sinking into the calcareous skeleton. At the stage shown in Figure 4 the tiny ampulla, still open to the outside, is an epidermally lined cavity. The structure in the center is composed of gastrodermal cells with a thin covering of epidermis.

The oögonia arise in the gastrodermal canals. Their precise site of origin is not known, but the distinctive cells can be seen inside the canals (Fig. 5). Meiotic divisions were not observed, so it was not possible to distinguish oögonia from

primary and secondary oöcytes. The eggs migrate along the gastrodermal canals to the developing ampullae, and one egg settles between the epidermis and gastrodermis (Fig. 5). Often other eggs are seen close to the ampullae or even at the base of the gastrodermal supporting structure, but only one settles at the position shown. The others probably degenerate. This stage of development, with the tiny egg between the gastrodermis and epidermis, is seen at all times of the year. Apparently more than a year can elapse before the egg begins to grow.

In late December and January the gastrodermal supporting structure, called the trophodisc, begins to increase in size and a distinct lumen becomes visible. Tiny yolk granules appear in the cytoplasm of the egg. The ampulla must increase in size to accommodate the growing egg and trophodisc. This is probably accomplished by dissolution of the surrounding calcareous skeleton. The nucleus of the egg is very distinct, measuring some 30 μ in diameter, and the tiny pore to the outside of the ampulla, diameter 16 μ, is still open.

Through February, March and April the trophodisc further increases in size (Fig. 6). The gastrodermal structure repeatedly outpockets, giving the appearance of numerous blind tunnels. More yolk is deposited, seeming to coalesce to form much larger granules. The largest granules are proximal, while the smaller ones are found at the distal side of the egg. The nucleus is still visible in a position near the distal edge of the egg, always very near the pore leading to the outside. The sperm probably enter the ampulla via this opening, the fertilization canal.

The egg remains at this stage until fertilization, which occurs some time in late May, June, or early July. Actual fertilization was never observed, but after an egg has been fertilized the nucleus is no longer visible, and the fertilization canal closes. The trophodisc begins to diminsh in size and completely degenerates within a few weeks.

The first visible sign of cleavage is a layer of cells at the distal edge and along the sides of the yolk. The yolk does not divide. In later stages these undifferentiated cells surround the yolk completely. As development proceeds, these cells differentiate into columnar epithelial cells with clear cytoplasm at the top and dense granules at the base (Fig. 7). These columnar cells appear first at the distal margin of the embryo, then at the sides, and finally along the proximal margin. Numerous small cells, presumably gastrodermal cells, are seen in the yolky area. Their origin and time of migration is not certain. The epidermal cells continue to increase in size for about two months. The mature, oval-shaped planula larva is 0.5–1 mm in length. Sometimes it must bend back on itself to fit in the tiny ampulla. The escape route for the planula develops after the fertilization canal closes. This is a new opening from the ampulla which opens into a nearby cyclosystem between two dactylozooids. In two favorable instances serial sections were obtained of planulae escaping through this canal. Release of the planulae occurs in late October, November, and early December.

The ampulla left by the escaped planula does not go to waste. Even while the planula is developing, a tiny new trophodisc is forming at the bottom of the ampulla as gastrodermis pushes into a thickened epidermal cell layer. The developing planula grows around this structure (Fig. 7). A new egg migrates to the area and is in position before the planula escapes. In this way the ampullae are used repeatedly.

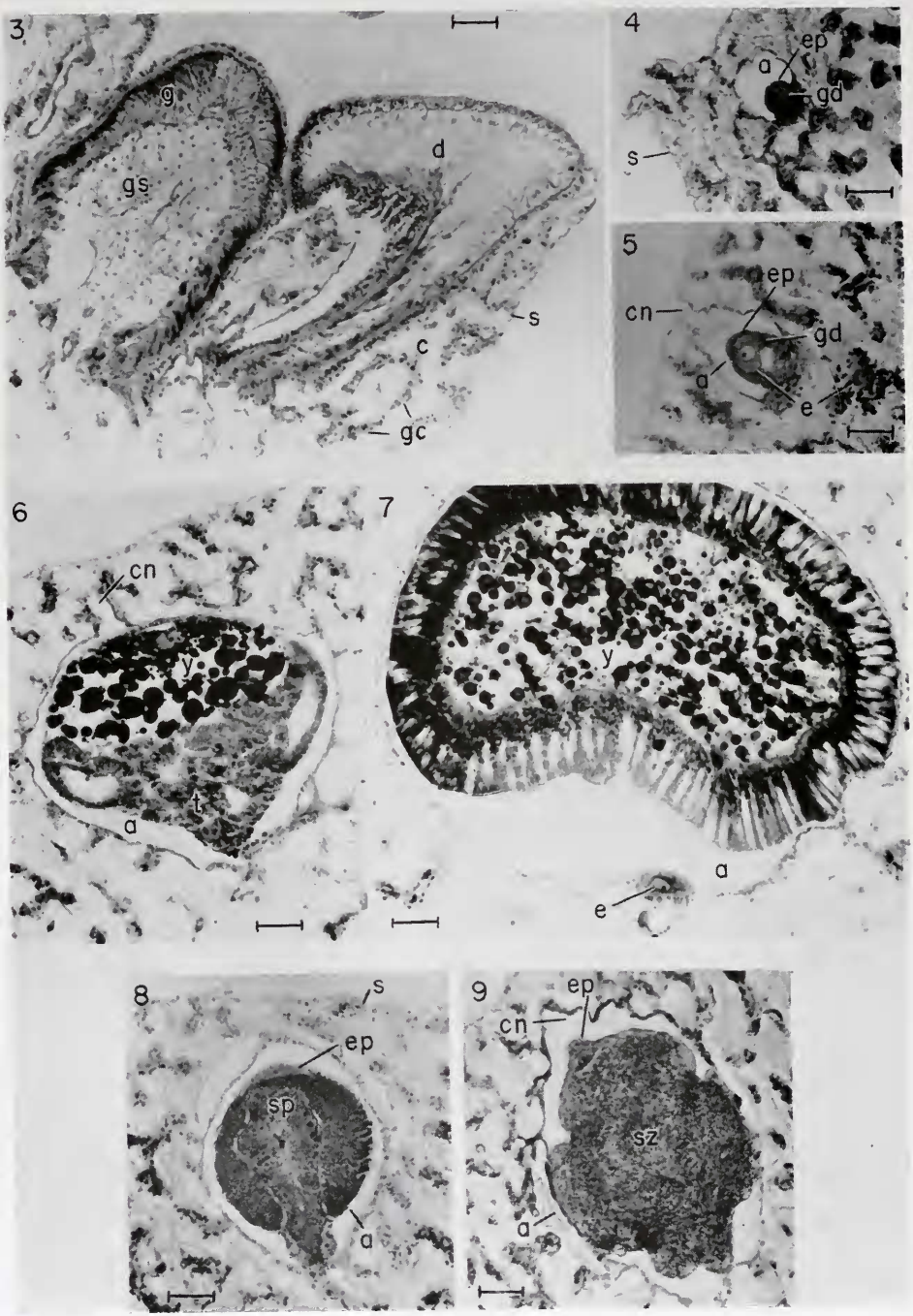

FIGURE 3. Photomicrograph of an actual longitudinal section through a cyclosystem. Zooids are only partially expanded.

The male gonophores also develop in ampullae. New male ampullae arise in the same way as do female ampullae (Fig. 4). The chamber is usually closed by a lid of tissue in the male ampulla. Spermatogonia arise in the gastrodermal canals and migrate to the developing ampulla, settling between the gastrodermis and epidermis. The cytological events of meiosis were never seen, so spermatogonia, and primary and secondary spermatocytes could not be identified.

Small ampullae with male germ cells are present at all times of the year, indicating, as in the females, that gonophores need not form and mature in a single year. In November and December the male gonophores begin to develop, with the gastrodermis forming a supporting structure, called a spadix, with a large lumen. The cells destined to become sperm cells increase in number, possibly by cell division or by further migration from the gastrodermal canals (Fig. 8). The ampulla is still closed to the outside at this stage.

The gonophores increase in size to about 500 μ. Starting in late February and continuing through April, the cells undergo a change in which the nuclei stain very darkly and are very tightly packed. They remain this way for 4–6 weeks.

Starting in late April the darkly staining cells change into spermatozoa (Fig. 9). In favorable sections sperm sacs containing both darkly staining cells and spermatozoa were seen. The opening to the outside is still barred by a plug formed by layers of epidermal cells at the distal end of the sperm sac. The gastrodermal spadix degenerates, leaving a sac full of sperm.

Spermatozoa are released in June and July. Actual release was seen only once in the histological sections with many sperm free in the ampulla and the sac apparently in the process of decreasing in size. The epidermal plug had opened, allowing the sperm to be released from the sac. Presumably the sperm are carried by currents to nearby female colonies where they enter the ampullae via the fertilization canals to reach the eggs.

Once the sperm are released, the gonophore for the following year begins to form. A new gastrodermal spadix is visible in late summer, usually with only a few germ cells present. No further development is visible until November or December.

The graph in Figure 10 shows the results of gross examination of the colonies. The mean, range, and standard deviation for egg and planula sizes are indicated.

FIGURE 4. Section through the edge of a colony showing a developing ampulla prior to the migration of gametes to the gonophore. Similar development is seen in both male and female colonies.

FIGURE 5. Photomicrograph of an undeveloped egg in the gonophore. Eggs at this stage of development are present throughout the year. Note the egg in the gastrodermal canals.

FIGURE 6. Fully developed female gonophore as typically seen in April and May. The egg nucleus is still visible, close to the proximal end of the fertilization canal.

FIGURE 7. Section through a developing planula showing the distinctive columnar epithelial cells surrounding the yolk. A new gonophore is developing under the planula.

FIGURE 8. Developing male gonophore typical of those seen in January with many future sperm cells in the sac.

FIGURE 9. Photomicrograph of a sperm sac containing spermatozoa. This is typical of male gonophores in May. Abbreviations used in Figures 3 to 9 are: a, ampulla; c, calcareous skeleton; cn, canal opening to the surface of the colony; d, dactylozooid; e, egg; ep, epidermis; g, gastrozooid; gc, gastrodermal canals; gd, gastrodermis; gs, gastrostyle; s, surface of the colony; sp, spadix, sz, spermatozoa; t, trophodisc; y, yolk. Scale equals 50 microns.

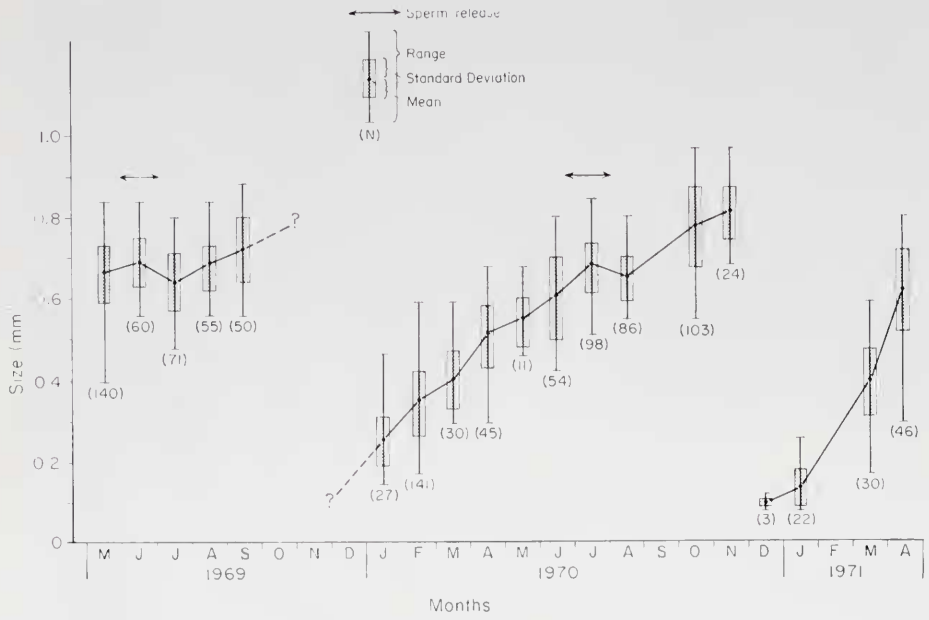

FIGURE 10. This figure shows the average egg or embryo size at different times of the year in *Allopora californica*. See text for further explanation.

There were always eggs present without yolk as indicated earlier (see Fig. 5). These ranged from 40–60 μ in size and could not be seen with the dissecting microscope. Figure 10 represents only those eggs in which yolk deposition had begun, those eggs which would be fertilized and would develop within that year. The double arrow indicates the period of sperm release and, presumably, of fertilization. From this point on, the size measured was that of a developing planula. The break in the graph, October through December 1969, was the period when collections were impossible as the Carmel beaches were closed because of pollution. The probable course of events during late 1969 has been indicated by a broken line.

Within the *Allopora californica* population at the two research sites there was variation in the size of the eggs or planulae at any given time, but there was very little variation in the stage of development. All the eggs began to deposit yolk at about the same time. Essentially all the eggs were fertilized within a 3–4 week period, and development of planulae progressed at a similar rate in all the colonies examined. Most of the planulae escaped in late October and November. A few (3) eggs showed yolk deposition in December 1970, but most showed no sign of growth until January 1971.

Settlement and mortality of new colonies

Eight separate plots totaling almost 4.5 square meters of surface area were studied. When planulae are released, they crawl or are carried by currents away from the parent colony and settle where space permits. A newly settled colony is flat, but even at this early stage the beginning of a depression where the first

cyclosystem will form is visible. In four colonies known to be less than three weeks old, the first cyclosystem had already formed.

The maximum possible ages of newly settled colonies were used in constructing a survivorship curve. If an area was examined, say, October 1, November 1, and December 1, and if a new colony was first seen on November 1 but was gone December 1, then the maximum life span was recorded as from October 2 to November 30, or 60 days. Survivorship curves for those colonies which settled during the two years, 1969–1970 and 1970–1971 are shown in Figure 11.

In the curve representing the data for 1969–1970, the solid line indicates actual observations. The dashed portion of the curve, covering the period when direct observations were impossible because of the closing of the beaches, is an estimate assuming that the rate of disappearance was the same for both years of the study. The settlement date was estimated from details of the reproductive cycle and larval development observed through mid-September of that year. Heaviest mortality occurred in the first few months after settlement. At the end of the study, $1\frac{1}{2}$ years later, six colonies were still alive.

The data for 1970–1971 include observations on 128 new colonies. At the end of the study, 180 days later, there were 25 colonies left.

Several factors are responsible for the demise of small colonies of *A. californica*. In many cases they attach to unstable substrates or to short-lived organisms, such as algae or brittle bryozoans. The settling of particulate matter is extremely harmful to the young colonies, and many on horizontal surfaces are buried in this way. Those on vertical surfaces or in areas of heavy surge tend to fare better. Young

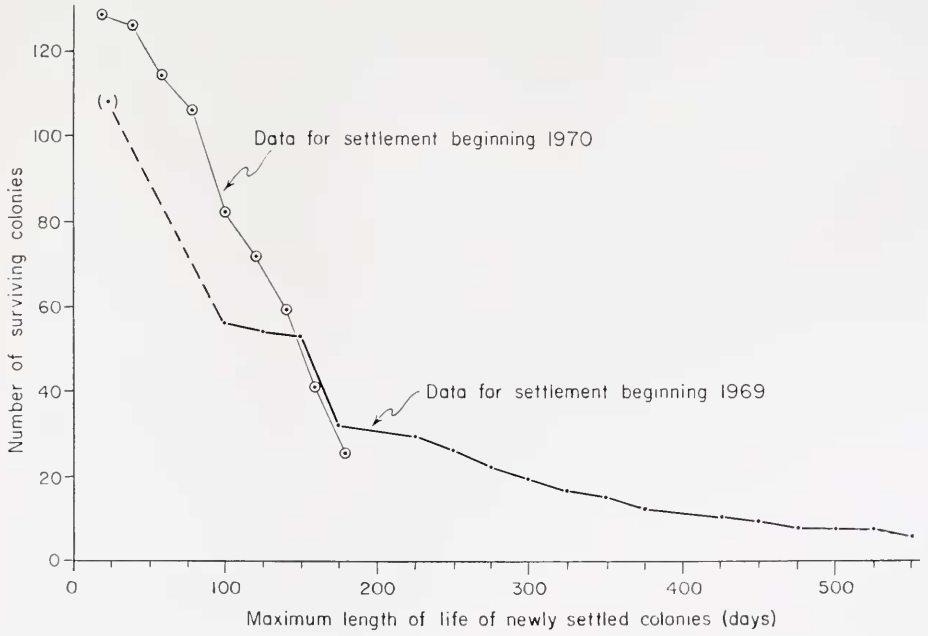

FIGURE 11. This figure shows survivorship curves for *A. californica* colonies settling in 1969 and settling in 1970. Dashed line indicates estimate. See text for further explanation.

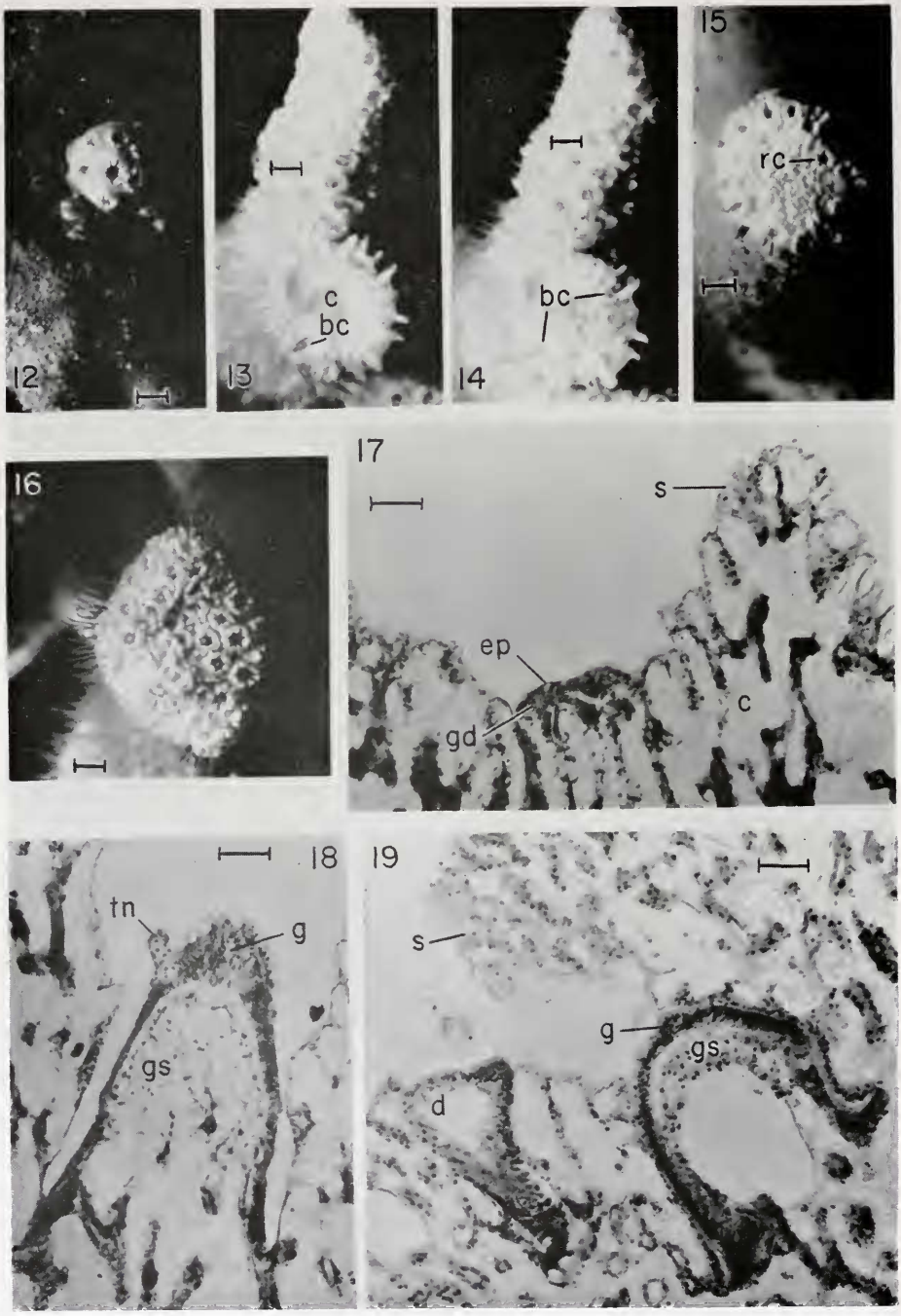

FIGURE 12. In water photograph of a one year old *A. californica* colony with several of its cyclosystems visibile. Note the newly settled barnacles crowding the coral.

colonies must compete with other benthic organisms for settling space. When algae begin to grow rapidly in the early spring, numerous colonies are overgrown. Barnacles and other organisms settling out of the plankton compete with the slow-growing *A. californica*. Figure 12 shows a typical one year old colony, only 5 mm across, with eight cyclosystems.

Regeneration

A newly cut branch of *Allopora* appears as seen in Figure 13. The broken edges are sharp, and the damaged cyclosystems stand out distinctly. The center of the branch is calcareous material. Within 7–14 days a change is evident (Fig. 14). The sharp edges are rounded, and the calcareous core is covered with tissue resembling very fine granulated sugar. This tissue covering continues to grow until it resembles fine sand grains on the tip of the branch. Within 4–6 weeks this granular appearance gives way to a series of ridges and furrows along the broken surface (Fig. 15). The cyclosystems broken in the original cut begin regenerating almost immediately and new cyclosystems are visible as early as 50 days after the cut is made. Broken cyclosystems reorient, if necessary, to resume growth in a direction compatible with the new orientation of the branch. Some reorient in an upward direction toward the new tip of the regenerating branch, while others resume growth outward toward the sides of the branch (Fig. 15). By comparing photographs of the same branch taken over a period of time, the new cyclosystems could be distinguished from those which existed prior to the cut. When new cyclosystems cover most of the available area, upward growth resumes (Fig. 16). This is usually 4–5 months after the branch is broken. The whole tip may grow, or the regenerating area may send up one or more branches with diameters less than that of the original branch.

Periodically the regenerating branches were broken off, fixed, and prepared for histological examination. Within a few days after the original break, the surface is invaded by numerous gastrodermal canals and an epidermal covering layer. The easily-visible granular appearance and ridges result from different

FIGURE 13. In water photograph of a newly cut branch of *Allopora californica* showing several broken cyclosystems. The central portion of the cut branch is calcareous material.

FIGURE 14. The same branch as seen in Figure 13 photographed 14 days after the branch was cut. The central calcareous core has been covered by living tissue.

FIGURE 15. Regenerating branch photographed on Day 56. The tissue covering the central core appears as ridges and furrows. A regenerating cyclosystem on the right has reoriented to grow upward toward the new surface of the branch.

FIGURE 16. Regenerating branch on Day 235 covered with new cyclosystems. Note the extended dactylozooid tentacles.

FIGURE 17. Photomicrograph of a regenerating branch showing the initial appearance of a new gastrozooid marked by a meeting of epidermis and gastrodermis at the surface of the colony.

FIGURE 18. Section through a new gastrozooid showing further development, including the appearance of one of the minute tentacles on the side of the gastrozooid.

FIGURE 19. Longitudinal section through a complete, tiny, new cyclosystem found on a regenerating branch tip. Abbreviations used in Figures 12 to 19 are: bc, broken cyclosystem; c, calcareous skeleton; d, dactylozooid; ep, epidermis; g, gastrozooid; gd, gastrodermis; gs, gastrostyle; rc, regenerating cyclosystem; s, surface of the colony; tn, tentacle. Scale for Figures 12 to 16 equals 1 millimeter. Scale for Figures 17 to 19 equals 50 microns.

growth rates of the tissue and skeleton resulting in the pitted surface seen in Figure 17. A thickened mass of gastrodermis and epidermis signals the beginning of a new cyclosystem (Fig. 17). The regenerating branch tip continues to grow, leaving this tissue behind in an ever-deepening depression. At a later stage, the future gastrozooid is quite recognizable, complete with a tiny gastrostyle and minute tentacles (Fig. 18). Shortly thereafter, on the walls of the future cyclosystem, the dactylozooids appear. These also start as a meeting of gastrodermal and epidermal tissue layers. The tiny cyclosystem, about $\frac{1}{4}$ full size, is shown in Figure 19.

Discussion

The first work on reproduction in a hydrocoral was by Hickson (1888) on *Millepora plicata*. He described the origin of both male and female gametes in the epidermis lining the gastrodermal canals, including a detailed account of the cytological events of maturation. The male germ cells induce the formation of a male gonophore, usually in the dactylozooids. The fertilized eggs develop in the gastrodermal canals and later at the base of the gastrozooids without any formation of a gonophore. The ciliated larvae without any yolk are released at an early stage. In another species, *Millepora murrayi*, a male gonophore develops, but the eggs develop solely in the gastrodermal canals.

In studying the stylasterine corals, Hickson (1890, 1891) suggested that the gametes cause local irritation in the gastrodermal canals, resulting in the outpocketing of tissue to form gonophores. Gametes in the ampullae are covered by a double sheath of epidermis and gastrodermis and are supported by a trophodisc in the female and a spadix in the male. Sperm enter the female colony via the mouth of the gastrozooids and migrate along the canals to fertilize the egg. Hickson described early planula development, and mentioned the re-use of the female ampullae year after year.

Reproduction in three species of stylasterine corals was described by England (1926). She found that the ampullae form at the surface of the colony where epidermis and gastrodermis meet and form a thickened tissue layer. In contrast to Hickson (1890, 1891), England did not find a double sheath covering the gametes in the gonophore; there was only an epidermal covering and a gastrodermal supporting structure with the egg or sperm between the two layers.

Goedbloed (1962) discussed the origin and development of gonophores in *Allopora blattea* and *Stylaster roseus*. She, too, concluded that the ampullae form at the surface of the colony, and she suggested that the germ cells induce their formation.

The work discussed above was limited to specimens from isolated collections, not allowing repeated observations to determine seasonal changes. The present investigation has been done on material collected monthly over a period of two years, giving a dimension of time to the study.

The ampullae of *Allopora californica* do form at the surface of the colony. With the available histological sequence, the course of events is quite clear; without it, Hickson's suggestion of ampulla formation from the inside out would look quite plausible. No evidence was found to support the assertion that gametes induce the formation of new ampullae. The new ampullae begin without any trace of gametes in the vicinity.

None of the previous workers suggested the dormancy of gonophores such as has been found in this study. Small ampullae with undeveloped future sperm and eggs were found throughout the year (see Fig. 5). All the maturing gonophores in each colony were at about the same stage of development at any one time. There was no indication that a second brood was produced later in the year, hence these immature gonophores must remain in this condition through a whole breeding season. What triggers the beginning or delay of maturation of a gonophore is not known.

Fertilization of the eggs in *A. californica* must be a complex process, since the sperm, released en masse, must travel to the ampullae of distant female colonies. Miller (1966) found evidence of chemotaxis during fertilization of the thecate hydrozoan, *Campanularia*. If a similar mechanism were present in *A. californica*, it would explain how tiny sperm can find the minute fertilization pore. Essentially all eggs examined after the period of sperm release were fertilized; only a very few seemed to be degenerating rather than developing.

The re-use of ampullae year after year is obviously a useful adaptation. Building an ampulla within a calcareous skeleton is a metabolically demanding task. The ampulllae are probably used for several years. As the colony increases in diameter, some are filled in with calcium carbonate and left behind.

A regular yearly cycle of sperm and egg production, fertilization, development, and release of the planulae is clearly demonstrated in *Allopora californica* (see Fig. 10). It is difficult to say what might trigger the cycle. Water temperature is very constant at Carmel, varying haphazardly between 8° C and 12° C at the depth of the study sites. There is rarely any thermocline in Carmel Bay at the depths investigated. Water turbidity is variable, with visibility varying radically even on the same day. Algal growth has a regular cycle with the short algae appearing in March, only to be cut off from the light by the giant kelp, *Macrocystis integrifolia* in June. Which, if any, of these environmental factors influence *Allopora* has not yet been determined. Grigg (1970) found that the reproductive cycle in the gorgonian *Muricea* was different in populations at different depths, possibly correlated with temperature differences. In a very few samples of *Allopora californica* taken from various depths there did not appear to be any difference in development of gonophores or larvae, but a more rigorous study is needed to demonstrate this conclusively.

Dr. Harry K. Fritchman of Boise State College, Boise, Idaho (personal communication) is working on release and settlement of *Allopora petrographa* larvae in the laboratory, including a histological study of the newly settled planulae. He has found that these larvae are heavily ciliated and capable of considerable muscular contraction. After pushing out of the ampullae, the larvae actively seek the bottom of the dish in the laboratory. If the same behavior obtains in the field, then the larval life of *Allopora* would be very brief. Since the appearance of the first newly settled colonies which were observed in the present study correlated very closely with the first histological observations of empty ampullae in the females, there is probably, at most, a very short planktonic stage. As Thorson (1950) points out, prolonging larval life allows greater mortality from predation and increases the risk of being swept away from suitable areas. Since *Allopora* planulae are lecithotrophic, the motile stages need not feed, but are available for dispersal.

Living in areas where currents and surge are fairly strong, many of the larvae would be swept away from suitable settling sites if the planktonic stage were very long. This suggests that the planulae settle quite soon after release, rather than enter the plankton.

From consideration of the survivorship curves (Fig. 11), it is obvious that any which settled and disappeared between the monthly observation dates could not be counted. Sometimes the initial level of a survivorship curve can be estimated by knowing the fecundity of the females in the population. Unfortunately, *Allopora californica* does not lend itself to determining this. The number of females cannot be determined since the sexes cannot be identified in the field. Further, the distribution of eggs within the female colony is haphazard. Measures of eggs/unit area and eggs/cyclosystem give such widely variable results as to be useless as an estimate of fecundity. From gross examination, however, the numbers of eggs per female colony are on the order of a few hundred.

The curves in Figure 11 show an initial steep drop in the number of surviving colonies, leveling off at 15–18 months. Those that live this long appear to have a good chance of surviving. The principle mortality, then, occurs during the settling stage and in the first year.

Survivorship curves for *Muricea* were calculated by Grigg (1970). If larval life is included, mortality is greater than 99%. If larval life is excluded, a constant mortaility rate is observed. The gorgonians, in contrast to *Allopora californica*, have a long larval planktonic stage, where most of the mortality takes place. In the study on *Muricea*, early settling stages were not so easily observed as they were in *A. californica*, so Grigg's settlement data may be a conservative estimate of the number which actually settled.

Mortality in young colonies of *A. californica* is often the result of competition for space and of the inability of the colonies to withstand sedimentation. The release of larvae coincides with the time of year when the algal cover is at a minimum and is prior to the settling of many attached benthic organisms, allowing a few weeks in which the incipient colonies may obtain a secure foothold. Sedimentation is a year-round problem. Horizontal surfaces are particularly vulnerable to this smothering by sediment. It is apparent that *A. californica* is best suited for surviving on vertical surfaces or in rocky crevices, away from algae, and where the currents and surge keep the rocks free of debris.

In large colonies of *A. californica*, mortality seems to be limited to mechanical abrasion and breakage. No evidence of predation was ever seen. On rare occasions a colony was seen which had died and which was being overgrown by encrusting organisms, but the reason for death was not apparent.

Other workers (Yonge, 1940; Stephenson and Stephenson, 1933; Grigg, 1970) have suggested that damaged Scleractinian and other corals do regenerate. Only Stephenson and Stephenson (1933), who stated that in branching forms regeneration occurs rapidly to fill in the gap and restore symmetry to the colony, elaborate on any mechanism of regrowth. Since the study of regeneration involves repeated visits to the same colony *in situ*, it is not surprising that information on other species is lacking.

It has generally been accepted that new cyclosystems arise by budding in *Allopora* (Mosley, 1876, 1879). But in the present study no evidence has been found

to suggest that budding is involved in asexual reproduction. *De novo* origin of new gastrozooids and dactylozooids occurs at the surface of the colony both in normal and regenerating branch tips. The gastrozooid develops quite fully before new dactylozooids begin to form, possibly induced by the presence of the new gastrozooid.

Cyclosystems must constantly redirect their growth to stay at the edge of the colony. As the branch grows, one would expect to find much wider spaces between cyclosystems at the base than at the tips of the branches. Such is the case in *Pocillopora damicornis* (Wainwright, 1963). Although this is true to some extent in *Allopora,* it is evident that new cyclosystems can arise along the sides of a branch. Usually the cyclosystems in any given area are about the same size. From time to time a much smaller cyclosystem is found, suggesting that it is much younger than the rest in the area.

The data obtained in this study provide basic information on the biology of *Allopora californica.* Future work, both in the field and the laboratory, may be aimed at answering such questions as how far the sperm can travel to a female gonophore, how the sperm locate the gonophore aperture, whether the larvae swim or creep to a settling site, and what induces the formation of new cyclosystems.

It is a pleasure to thank Dr. Cadet H. Hand, Jr. and Dr. Ralph I. Smith of the Department of Zoology, University of California, Berkeley, for encouragement and helpful suggestions. Mrs. Emily Reid prepared Figures 1, 2, 10, and 11. Special thanks are due to Mr. Lloyd F. Austin, first, for his advice as Department of Zoology Histological Microtechnician, and second, for his support as the Berkeley Campus Diving Officer. He introduced me to SCUBA diving and showed me its potential as a research tool for a marine biologist. The Diving Safety Program, which he heads, was instrumental in the success of the project. Over 40 U. C. certified divers helped with the project in numerous ways. Miss Penelope Hermes, Mr. Robert Loew, and Dr. John Z. Ostarello deserve special mention for the time they spent working with me as diving partners. I was supported in part during this study by a National Science Foundation Graduate Fellowship.

Summary

1. The life history of the hydrocoral *Allopora californica* has been studied over a two-year period. The formation of male and female gonophores is described and the maturation of sperm and eggs within these is illustrated.

2. Eggs are fertilized within the ampullae in the female colony. Subsequent larval development is described. The yearly cycle of sperm and egg maturation begins in January and culminates with release of planula larvae in November.

3. Field observations to study settlement and mortality of young colonies showed that only a very small percentage of them survive a full year. Competition for space and smothering by sediment are two main factors accounting for the high mortality.

4. The process of regeneration in the hydrocoral was studied using photography in the field combined with histological study in the laboratory. After a branch is

cut the broken end has sharp edges and many damaged cyclosystems. Within a week new tissue has covered the wound, and new cyclosystems are visible after 7–8 weeks. Upward growth resumes 4–5 months after a branch has been cut.

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